An analysis of the community structure of subtidal and intertidal benthic mollusks of the Inlet of Baño (Ría de Ferrol) (northwestern Spain)

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Abstract: A study of the benthic communities of the Inlet of Baño (Ría de Ferrol) (northwestern Spain) was carried out, encompassing the examination of 75 sampling stations (35 subtidal and 40 intertidal). Data were subjected to classification and ordination techniques. Two major assemblages were identified, and divided into five subgroups in terms of dominance of the species, constancy, and fidelity. The subtidal zone was characterized by the *Abra alba* (Wood, 1802) community. It was structured in facies as follows: The *Nucula nitida* Sowerby, 1833-*Thyasira flexuosa* (Montagu, 1803) facies, was the innermost, in the eastern area of the inlet; another facies existed in the transition toward the *Clausinella fasciata* (da Costa, 1778) community in the outer inlet area. In the intertidal zone the *Cerastoderma edule* (Linné, 1758)-*Scrobicularia plana* (da Costa, 1778) community was defined, which was also structured in facies: one facies, located at the mouth of the river, was dominated by *Hydrobia ulvae* (Pennant, 1777); another facies, found in the inner inlet area associated with a meadow of the seagrass *Zostera noltii* Hornem., 1832, characterized by *Bittium reticulatum* (da Costa, 1778), *Loripes lacteus* (Linné, 1758), *C. edule, Venerupis senegalensis* (Gmelin, 1791), and *Rissostomia membranacea* (Adams, 1800), and a third facies, situated at the border of the inlet, included *Gibbula umbilicalis* (da Costa, 1778), *Littorina littorea* (Linné, 1758), *L. obtusata* (Linné, 1758), *V. senegalensis*, etc., as dominant species. The analyses showed that sediment parameters (mainly grain size), organic matter in the subtidal stations, and grain size and depth are the most important factors governing the distribution and abundance of the communities.

Key words: community structure, intertidal, subtidal, mollusks, Ría de Ferrol, Spain

Research on the macrobenthic communities of the northern coast of the Iberian Peninsula has been carried out by several authors, who have taken both a faunistic and an ecological-descriptive approach. Their sources of information have been primarily articles on the ecology of the macrobenthos, and their ultimate goals have been to carry out analyses of the faunistic community as a whole. This is reflected by the great number of biocenotic studies on the benthos living on soft substrata in recent years on the Galician coasts (Viéitez, 1976, 1981; Anadón, 1980; Mora, 1980; Penas and González, 1983; Rodríguez Castelo and Mora, 1984; Planas and Mora, 1984 a, b; Laborda, 1986; Planas, 1986; López Serrano and Viéitez, 1987; Viéitez and Baz, 1988; Junoy and Viéitez, 1989, 1990; Mazé et al., 1990; Palacio et al., 1991, 1993; Currás and Mora, 1991, 1992; Pérez Edrosa and Junoy, 1993).

Frequent studies have also been made on the malacological communities of different geographical areas of the European Atlantic coasts (Lande, 1975; Evans and Tallmark, 1976; Petersen, 1977; Glémarec, 1978; Tunberg, 1981; Dewarumez, 1983; Gentil *et al.*, 1986; Cornet, 1985; Quintino et al., 1986; Sauriau et al., 1989).

However, despite the plethora of faunistic studies involving Galician mollusks, there is a need for research on their sinecology. An exception to the lack of sinecological studies is the work by Cadée (1968) in the Ría de Arousa. Therefore the purpose of this work was to study the ecology of the benthic populations of mollusks living on soft substrata, both subtidal and intertidal, of the Inlet of Baño (Ría de Ferrol, northwestern Spain). The aim was to define the different communities living in the inlet and how they relate to physicochemical factors (granulometry, sorting coefficient, organic matter, carbonates, and nitrogen).

MATERIAL AND METHODS

STUDY AREA

The Inlet of Baño (Fig. 1) is located on the southern border of the central channel in the Ría de Ferrol between the Punta do Faro da Palma (43°27'52"N; 08°16'49"W) and Punta Piteira (43°27'57"N;

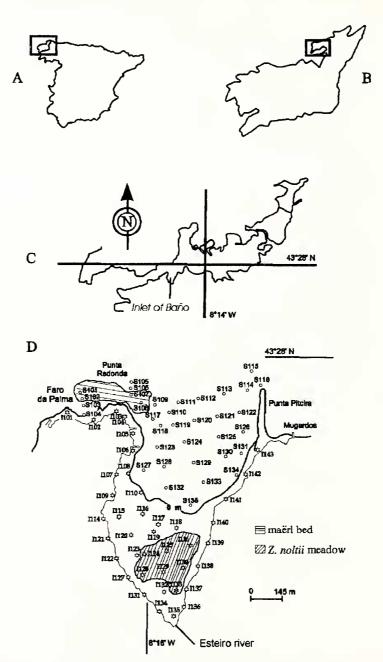


Fig. 1. Location of the 75 sampling stations in the Inlet of Baño (Ría de Ferrol), northwestern Spain. A. Spain. B. Galicia. C. Ría de Ferrol. D. Inlet of Baño. (I, intertidal station; S, subtidal station).

08°15'37"W), with an area of 0.5 km² and a maximum depth of 18 m (Fig. 2). The inlet is oriented in a NNE-SSW direction; the prevailing winds are southwesterly for most of the year, except in summer when northeasterlies become dominant. The mean tidal range in the ria is 2.7 m, and tidal effects give rise to strong currents (up to 1.5 m/s in the ria's central channel). Outward movement of water from the ria provokes flow to the southeast within the inlet, while movement into the ria provokes flow to the SSW within the

inlet. These currents, which are stronger at the mouth of the inlet than at more distal points, are the dominant factor affecting sediment distribution within the inlet (Fig. 3).

The inlet is characterized by soft bottom bordered by a rocky strip. A maërl bed is present in four of the western stations, between 4.5 and 10.5 m depth. A seagrass meadow of *Zostera noltii* Hornem., 1832, is present in the central intertidal zone.

The distribution of different grain sizes suggests an

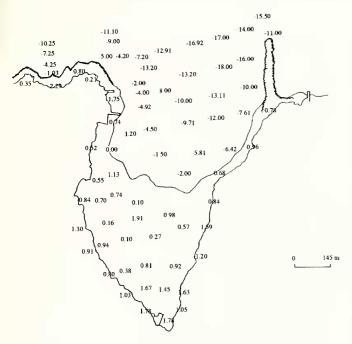


Fig. 2. Depth (m) of the subtidal (-) and intertidal (+) stations.

enrichment gradient for fine fractions on the eastern part of the Inlet of Baño. Sandy muds prevail in this area, while the coarsest sediment fractions are prevalent in the outer part. On the other hand, the percentages of organic matter are low, with enrichment toward the eastern part (Table 1). Nitrogen follows a variation pattern similar to that of organic matter. Calcium carbonate does not present a high percentage, with highest values found in the subtidal zone (Olabarria *et al.*, 1996).

The area has a temperate humid Atlantic climate and the hydrographic conditions show thermal variations of more than 5°C in the first 10 m. This variation decreases with depth. Salinity fluctuates with the tides and seasons, due to the fact that the ria has difficulty in draining because of the narrow central channel, which creates water masses having different salinities. The pH values are consistently between 7 and 9, and there are no anomalous data that would indicate a source of excessive acidity or alkalinity (COTOP, 1987).

SAMPLE COLLECTION

The sampling program, which was designed to provide sufficient information on the distribution of the different species of mollusks, consisted of 35 subtidal and 40 intertidal stations sampled from July 1991 to June 1992. Sampling points were selected along 12 parallel transects across the inlet at 100 m intervals, taking samples at the points that were judged by visual examination to show a change in nature, texture, or substrate covering. Intertidal samples were additionally collected at the ends of each transect and, in the inner intertidal zone, samples were also taken every 100 m along each transect (Olabarria *et al.*, 1996). In the subtidal zone, samples were collected by scuba diving. At each point, a 0.5 m² square sample was taken, to a depth of approximately 20 cm, using a rectangular shovel. All samples were subsequently wet-sieved through a series of sieves with 10, 2, and 0.5 mm mesh. Finally the sieved samples were transported to the laboratory, and the living specimens were sorted by the remounting technique (Ros, 1975). Sediment samples were obtained for granulometric study. This consisted of an analysis of grain size, organic matter, nitrogen, and carbonates (Guitian and Carballas, 1976).

DATA ANALYSES

Data were organized into station by species matrices. The Shannon-Wiener and Pielou's evenness indices (Washington, 1984) were used to assess species diversity and evenness.

The data for the population studies were processed in two ways: (1) Analyses of qualitative data (presenceabsence) of the species in the sampling stations were performed by applying the point correlation coefficient (Φ ; Daget, 1976), whereby a correlation matrix is created, followed by classification into clusters through the clustering algorithm UPGMA, by means of the NTSYS-pc program

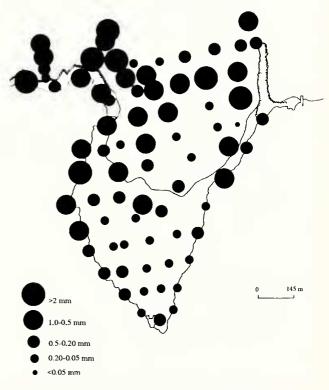


Fig. 3. Sediment characteristics of the Inlet of Baño (Ría de Ferrol). Mean grain size in mm.

Station	мо	CA	N	So	Station	мо	СА	N	So
SIOI	0.42	30.22	0.05	2.42	1103	0.59	19.64	0.08	> 2.50
S102	0.51	31.11	0.04	2.69	I104	0.43	20.57	0.04	1.80
SI03	0.42	33.33	0.03	1.76	I105	0.67	9.43	0.06	1.58
S104	1.03	18.22	0.06	6.06	1106	0.39	12.86	0.03	2.58
S105	0.70	34.67	0.08	4.80	I107	0.55	2.57	0.04	2.55
S106	1.04	8.89	0.01	8.36	1108	0.54	2.10	0.06	1.95
S107	1.99	32.44	0.13	6.44	I109	0.66	1.71	0.06	> 1.65
SI08	1.16	34.67	0.10	2.18	I110	2.00	8.57	0.06	3.71
S109	1.53	29.33	0.10	9.60	I114	0.23	1.71	0.02	> 1.29
S110	0.69	32.89	0.05	2.75	1115	0.47	1.03	0.03	1.79
SIII	1.69	32.00	0.13	0.18	I116	1.41	0.34	0.10	5.07
SI12	1.13	13.78	0.09	21.70	I117	0.63	26.67	0.08	3.77
S113	0.97	13.78	0.08	2.54	I118	0.34	16.29	0.05	2.92
S114	1.37	21.33	0.07	20.99	1119	0.59	0.86	0.01	1.63
S115	0.44	34.67	0.04	2.00	1120	0.94	0.34	0.02	1.49
SI16	0.58	34.67	0.04	1.78	II2I	0.91	0.86	0.07	> 2.50
SI17	0.32	4.89	0.03	2.08	II22	1.37	1.71	0.09	1.54
SI18	1.55	24.89	0.09	9.57	I123	0.64	0.26	0.03	1.89
SII9	0.44	17.33	0.03	2.63	II24	0.83	0.17	0.04	1.45
SI20	0.59	18.40	0.04	3.39	1125	0.83	0.26	0.04	1.37
SI2I	0.87	27.56	0.08	2.54	1126	0.43	1.03	0.02	1.27
SI22	0.60	30.22	0.07	7.50	I127	0.51	0.86	0.04	2.29
SI23	0.45	16.44	0.04	2.35	II28	0.82	0.34	0.02	2.23
S124	0.69	30.22	0.06	>3.30	I129	1.04	0.86	0.09	1.38
SI25	0.97	35.56	0.14	10.04	I130	1.23	0.26	0.05	0.32
S126	1.31	22.58	0.05	>3.90	1131	0.48	0.86	0.04	4.31
SI27	1.83	2.22	0.12	>1.84	II32	0.72	0.17	0.03	1.41
SI28	0.26	6.29	0.04	>3.50	I133	0.91	0.34	0.02	1.43
SI29	1.80	17.33	0.12	8.48	I134	0.91	0.26	0.03	1.32
S130	1.51	25.78	0.11	9.00	I135	0.49	1.03	0.02	1.50
SI3I	2	16.27	0.10	8.50	1136	0.44	0.17	0.35	1.77
SI32	0.61	1.33	0.04	1.61	I137	0.95	0.17	0.04	1.46
S133	2.04	6.22	0.11	5.21	1138	0.80	0.17	0.05	3.77
S134	0.93	19.02	0.03	>3.53	I139	0.76	0.86	0.07	3.92
S135	0.42	0.89	0.03	1.70	II40	0.63	0.86	0.05	7.17
1101	0.17	12.00	0.02	1.13	II41	0.69	4.29	0.06	3.08
I102	0.38	1.42	0.01	1.78	I142	0.38	24.89	0.03	1.58
					I143	0.78	14.23	0.06	3.65

Table I. Organic matter (MO), carbonates (CA), nitrogen (N) and sort coefficient (So; Trask, 1932) in subtidal and intertidal stations.

(ver. 1.60; Rohlf, 1990).

$$\Phi = \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}}$$

where a = number of species in both stations; b = number of species in the first station; c = number of species in the second station; and d = species absent in both stations. Φ values ranged from -1 to +1; p = a + b + c + d, $\chi^2 = p \Phi^2$.

(2) Analyses of quantitative data of the species present in at least 10% of the stations were performed, omitting those which could create "noise" because of their narrow distribution and scarcity. The Detrending Correspondence Analysis (DCA) was applied according to the polynomial method, by means of the CANOCO-pc program (ver. 3.10; Ter Braak, 1988). The data were transformed according to the formula, $x = log_{10} (x + 1)$. This technique plots the stations along the axes according to similarity in species composition. The axes are often interpreted as environmental gradients whose identity can be analyzed by means of statistical correlations between the location of the stations on the axes and their environmental characteristics (Eleftheriou and Basford, 1989; Junoy and Viéitez, 1990). The environmental variables measured were: depth (positive values for intertidal stations; negative values for subtidal stations), percentages of the different granulometric fractions, organic matter, silt-clay ratio, carbonates, nitrogen, and sort coefficient. These environmental

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Table 2. Species classifications according to constancy and fidelity indices. (C_{Aii} , addition of constancies of species A within each population; N_{A1} , number of stations within population where species A exists; N_1 , total number of stations within population).

Constancy index		Fidelity ind	ex			
$C_{A1} = (N_{A1} / N_1) x$	100	(C _{A1} / C _{Aii}) x 100				
		accidental	<10%			
rare	< 12%	occasional	11-33%			
not very common	13-25%	accessory	34-50%			
common	26-50%	preferential	51-66%			
very common	51-75%	elective	67-90%			
constant	76-100%	exclusive	91-100%			

factors were correlated with the axes through Spearman's correlation analysis.

Based on the group of stations defined using the point correlation coefficient, the species were classified according to the criteria of constancy and fidelity, based on number of species (Dajoz, 1971; Table 2), and fidelity-dominance product (FxD; Glémarec, 1964), including only species that appeared in at least two stations (Glémarec, 1964; Cabioch, 1968; Lastra *et al.*, 1990; Junoy and Viéitez, 1990; Currás and Mora, 1991).

RESULTS

FAUNISTIC ANALYSIS, SPECIES DIVERSITY, AND ABUNDANCE

The 75 samples analyzed yielded a total of 20,647 individuals belonging to 148 species, in which gastropods were the most abundant (62.4%; Table 3), followed by bivalves (36.7%); chitons and scaphopods were present in small numbers. The gastropods numerically dominated the intertidal zone, outnumbering the bivalves by more than twofold. This is probably caused by the large number of individuals belonging to abundant species such as *Hydrobia ulvae* and *Rissoa parva*. The latter was also present in the subtidal zone in a high number of samples along with *Hinia reticulata*, *H. incrassata*, and *Onoba semicostata*. There,

bivalves were slightly more dominant than gastropods, due to the high number of individuals of *Mysella bidentata*, in addition to *Papillicardium papillosum*, and several species of Anomiidae. The bivalves *Mytilus edulis* and *Venerupis senegalensis* were the most abundant species in the intertidal zone. [Note: The species *Littorina littorea*, *L. obtusata*, *L. mariae*, *Lepidochitona cinerea*, and *M. edulis* are normally associated with hard bottoms. In some cases during this study, small stones were included in the soft sediment samples collected by shovel from the Inlet of Baño. These small stones provided hard substratum for the chitons, and also for attached algae, thus providing food for the periwinkle species.]

The values of the Shannon-Wiener diversity index (Table 4) fluctuated between 0.00 (station 1134) and 4.35 (station S112), and evenness ranged from 0.06 (station 1135) to 0.94 (station S124). These two parameters were positively correlated (r = 0.57; p < 0.001).

Diversity correlated positively with carbonate content, percentage of coarse sand, and sorting coefficient, and negatively with depth and percentage of fine sand. Both relative diversity and evenness showed positive correlations with the percentage of coarse sand, percentage of gravel, and the sort coefficient, and a slightly negative correlation with the percentage of fine sand (Table 5).

The lowest population density was recorded at station I135 with 32 ind/m², and the highest density at station S111 (6,040 ind/m²). The mean density in the subtidal zone (1,294.6 ind/m²) was higher than that in the intertidal zone (931.9 ind/m²).

Species richness varied widely, with a greater number of species in the subtidal than in the intertidal zone. The lowest values for species richness were found at the intertidal stations near the mouth of the river, due to high abundance of the dominant species *Hydrobia ulvae*. Species richness correlated negatively with the percentage of fine sand and positively with carbonate content, and percentages of coarse sand, gravel, and silt-clay, which explains the increase in species richness at the outer subtidal stations with coarser grain size and higher silt-clay percentages.

Table 3. Number of individuals (ind) and species (sp), and total percentage (%) of individuals in the subtidal and intertidal zones and in both.

		TOTAL			JBTIDAL		INTER	TIDAL	
	ind	sp	%	ind	sp	%	ind	sp	%
Polyplacophora	177	6	0.85	110	6	0.99	67	4	0.72
Gastropoda	1,288	89	62.39	5,206	82	45.95	7,676	41	82.37
Scaphopoda	9	1	0.04	9	1	0.07	0	0	0.00
Bivalvia	7,579	52	36.70	6,003	52	52.99	1,576	32	16.91
TOTAL	9,053	148	100.00	11,328	141	100.00	9,319	77	100.00

Table 4. Faunistic parameters for each subtidal and intertidal station: abundance, species richness (R), Shannon-
Wiener diversity index (H'), Pielou's evenness index (J'), and density (ind/m ²).

Station	Abundance	R	H'	J,	ind/m2	Station	Abundance	R	H'	l,	ind/m2
S101	273	31	4.25	0.86	1,092	1103	530	29	3.17	0.62	2,120
S102	194	29	3.61	0.74	776	I104	249	24	3.46	0.75	996
S103	158	20	3.09	0.72	632	I105	162	12	2.28	0.63	648
S104	112	19	3.43	0.81	448	I106	165	13	2.60	0.70	660
S105	204	27	3.85	0.81	816	I107	481	23	3.11	0.69	1924
S106	924	37	3.74	0.72	3,696	I108	154	11	2.37	0.68	616
S107	461	36	3.82	0.74	1,844	I109	387	17	3.48	0.85	1,548
S108	1,188	39	3.26	0.62	4,752	I110	56	8	2.11	0.70	224
S109	658	38	3.15	0.60	2,632	I114	152	17	2.68	0.66	608
S110	260	32	4.07	0.81	1,040	I115	12	5	2.12	0.91	48
S111	1,510	45	2.81	0.51	6,040	I116	56	16	3.08	0.77	224
S112	365	42	4.35	0.80	1,460	I117	274	25	3.21	0.69	1,096
S113	802	49	4.19	0.75	3,208	I118	79	18	3.24	0.77	316
S114	553	43	4.24	0.78	2,212	I119	10	4	1.85	0.92	40
S115	218	33	4.11	0.81	872	I120	24	9	2.43	0.76	96
S116	523	29	2.87	0.59	2,092	I121	140	8	2.14	0.71	560
S117	264	19	2.95	0.69	1,056	I122	271	17	2.43	0.59	1,084
S118	231	21	2.24	0.51	924	I123	143	11	3.06	0.88	572
S119	127	24	3.39	0.74	508	I124	343	14	2.11	0.55	1,372
S120	48	15	3.38	0.86	192	I125	363	13	1.78	0.48	1,452
S121	85	24	3.00	0.65	340	I126	442	13	1.61	0.43	1,768
S122	369	33	2.87	0.57	1,476	I127	62	12	2.92	0.81	248
S123	112	22	3.51	0.78	448	I128	53	9	2.59	0.82	212
S124	29	15	3.69	0.94	116	I129	734	9	0.44	0.14	2,936
S125	96	21	2.46	0.56	384	I130	204	13	1.72	0.46	816
S126	337	29	3.58	0.37	1,348	I131	199	9	1.38	0.44	796
S127	40	8	2.39	0.79	160	I132	388	4	0.20	0.10	1,552
S128	70	16	3.25	0.81	280	I133	802	8	0.30	0.09	3,208
S129	82	21	3.84	0.87	328	I134	45	1	0.00	_	180
S130	379	33	2.82	0.56	1,516	1135	8	3	1.06	0.07	32
S131	126	21	3.57	0.81	504	I136	171	1	0.00	_	684
S132	110	10	1.58	0.47	440	I137	746	2	0.06	0.06	2,984
S133	205	26	3.28	0.69	820	I138	400	11	2.49	0.72	1,600
S134	131	18	2.50	0.59	524	I139	56	9	2.83	0.89	224
S135	84	8	1.94	0.65	336	I140	20	6	1.94	0.75	80
I101	142	24	3.99	0.87	568	I141	146	13	2.21	0.59	584
I102	333	24	3.41	0.74	1,332	I142	131	20	3.41	0.79	524
						I143	186	21	3.48	0.79	744

COMMUNITY STRUCTURE

The classification (Fig. 4) that was obtained after applying the point correlation coefficient for 99% significance ($\Phi = 0.29$) showed two large assemblages (A and B) which belong to the intertidal and subtidal stations, respectively. These assemblages were divided into five subgroups: A1, A2, A3, B1, and B2. Subgroup A1 (five stations) located in the inner part of the inlet near the mouth of the river; subgroup A2 (18 stations) included a group of intertidal stations located along the border of the inlet; subgroup A3 (17 stations) included the intertidal stations of the central zone, mostly covered by *Zostera noltii*, which also comprised two subtidal stations; subgroup B1 (ten stations) located in the middle-eastern subtidal zone; subgroup B2 (23 stations) consisted of the outermost subtidal stations which are subjected to stronger hydrodynamism.

A non-parametric Kruskal-Wallis test proved that there were significant differences between assemblages A and B in terms of the percentages of fine sand, carbonates, and silt-clay, the sort coefficient, and diversity (p < 0.001), as well as the percentages of coarse sand, gravel, and organic matter (p < 0.05). Assemblage B stations had higher mean percentages of gravel, coarse sand, silt-clay, and carbonates than assemblage A. It also surpassed assemblage A in the mean percentage of organic matter, mean diversity value, and sort coefficient. However, assemblage A stations exhibited higher percentages of fine sand than those of assemblage B. The same analysis was later applied to the different subgroups and a multiple comparison test (Conover, 1971) was carried out *a posteriori*, to reveal the

Table 5. Spearman's rank correlations between ordination axes and community index, and environmental variables in Inlet of Baño. Depth (measured in relation to zero tidal level): subtidal stations (-m) and intertidal stations (+m). (H', Shannon-Wiener diversity index; J', Pielou's evenness index; R, species richness; *, p < 0.05; **, p < 0.01; NS, not significant.).

				Sub	tidal	Inter	rtidal
Environmental variables	R	J	H'	Axis l	Axis II	Axis I	Axis 11
Gravel	0.44**	0.33**	0.51**	-0.29NS	-0.14NS	-0.20NS	-0.52**
Coarse sand	0.43**	0.35*	0.52**	-0.39*	0.62**	-0.13NS	-0.64**
Medium sand	-0.15NS	0.04NS	-0.09NS	-0.05NS	0.10NS	-0.08NS	-0.04NS
Fine sand	-0.69**	-0.24*	-0.69**	0.66**	-0.25NS	0.27NS	0.67**
Carbonates	0.78**	0.13NS	0.66**	-0.59**	-0.40**	-0.05NS	-0.67**
Organic matter	0.14NS	-0.19NS	-0.01NS	0.32NS	-0.52**	-0.21NS	0.12 ^{NS}
Nitrogen	0.41**	-0.03NS	0.25*	0.22NS	-0.47**	-0.04NS	-0.22NS
Silt-clay	0.45**	-0.04NS	0.27*	0.18NS	-0.17NS	0.29NS	0.05NS
Depth	-0.68**	-0.13NS	-0.56**	0.05NS	-0.06NS	-0.39*	0.32*
Sort coefficient	0.44**	0.30*	0.50**	-0.41*	-0.16NS	-0.09NS	-0.41**

groups that significantly differed from one another in the different parameters (Table 6).

The ordination analysis (DCA) was carried out on the subtidal and intertidal stations as a whole. However, because of the excessive concentration of points in the upper and lower quadrant of the negative part of axis I, a separate analysis for the subtidal and intertidal samples was performed. These analyses were based on the groups derived from the application of the point correlation coefficient for a 99% level of significance.

In the analysis of the intertidal stations, the first two axes accounted for 36.4% of the total variance (Fig. 5). Axis I had a slightly negative correlation with the depth parameter, and axis II correlated positively with the percentage of fine sand and negatively with the percentage of carbonates and coarse sand (Table 5). In this analysis there are three groups of stations; on the positive side of axis I, both in the upper and lower quadrants, there is a group of stations that in the similarity (Φ) and constancy-fidelity analyses distinguished subgroup A3. In the upper left-hand quadrant, there was a group of closely-linked stations for which the most characteristic species was Hydrobia ulvae. This species reached densities of 2,960 ind/m² (station 1137). This group defined subgroup A in the similarity analysis. Below, in the upper left-hand quadrant which continued onto the lower quadrant, there was a group of stations and species that characterized what has been defined as subgroup A2 using the point correlation and the constancy-fidelity indices.

In the analysis of the subtidal stations, the coordinates of the first two axes accounted for 33.4% of the total variance (Fig. 6). Axis I had a high positive correlation with the percentage of fine sand and carbonates, and axis II displayed a correlation with the percentage of coarse sand and organic matter, and to a lesser extent with the percentage of carbonates and nitrogen (Table 5). In this analysis, a group of stations and species defining subgroup B1 can be seen in the upper and lower right-hand quadrants, located toward the positive end of axis I. On the negative side of axis I, in both the upper and lower quadrants, there is a group of stations and species that has been defined by the similarity index (Φ) and the constancy and fidelity indices as subgroup B2. In the vicinity of this group there is a group of stations (S126, S122, S112, S118, S130, S134) which are transition stations, grouped in the same cluster in the point correlation analysis (subgroup B2). These are stations with modified bottoms, although originally they most likely had bottoms similar to the stations in subgroup B1. However, due to dredging operations, sediments from other

Table 6. Multiple comparison test (Conover, 1971) between the subgroups derived from the point correlation analysis (A1, A2, A3, B1, B2) indicating groups that showed no significant differences (p < 0.01).

Gravel percentage	Coarse sand percentage
A1 < A3 < B1 < B2 < A2	A1 < A3 < B1< A2< B2
Fine sand percentage	Silt-clay percentage
B2 < A2 < B1 < A3 < A1	A1 < A2 < A3 < B1 < B2
Carbonates percentage	Diversity index
A1 < A3 < A2 < B1 < B2	A1 < A3 < A2 < B1 < B2
	÷

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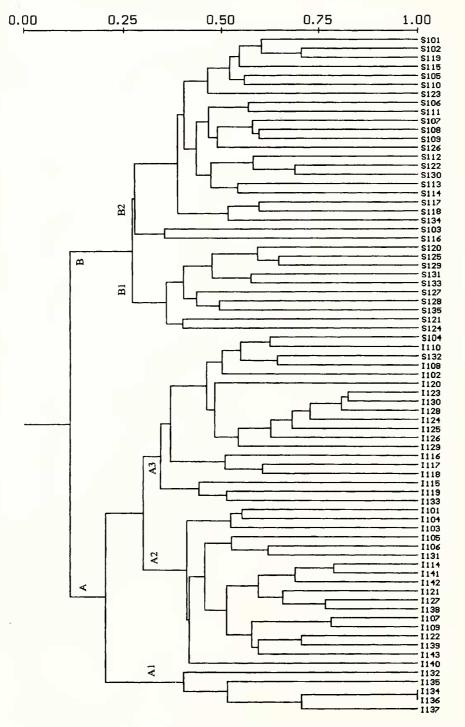


Fig. 4. Clusters of the samples based on the point correlation index and sample of the five main groups.

areas of the ria were deposited there.

After applying the entire series of statistical analyses, a clear coherence can be seen among them, with very similar results obtained from the different methods. A correspondence between the classification analysis (similarity coefficient, Φ) and the ordination analysis (DCA) was found. The results point to the presence of five groups (Fig. 7) characterized as follows:

Subgroup A1 was located in the intertidal zone close to the mouth of the river. It consisted of five stations in which 13 species were found (Table 7). This area had predominantly fine sands ($62.43\% \pm 6.04\%$) and the lowest

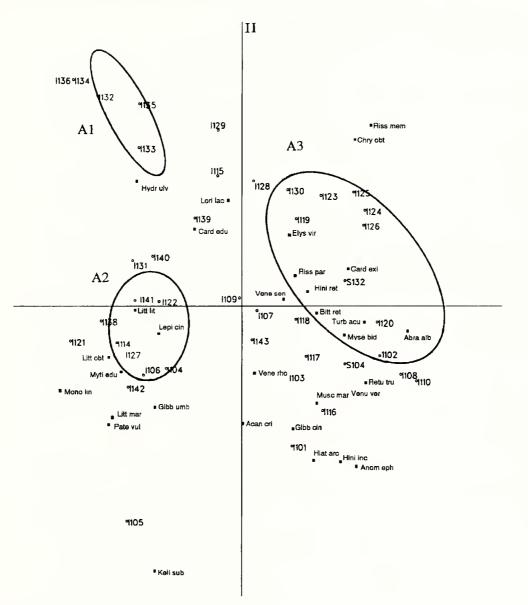


Fig. 5. Stations and species arranged according to axes I and II of the correspondences analysis (DCA) for the intertidal stations, showing the division into three main groups, confirmed by the confidence ellipsis method (Sokal and Rohlf, 1979). Species codes as in Table 7.

mean diversity values (0.53 ± 0.79) . Evenness was between 0.91 (station II15) and 0.06 (stations II35, II37), even though this index was undetermined (H' = 0) in two stations by the exclusive presence of the gastropod *Hydrobia ulvae*, which reached very high densities in this subgroup (2,960 ind/m²). There was a small number of species which varied from 5 (station II15) to 1 (stations II34, II35). In this subgroup, the presence of a freshwater bivalve *Pisidium casertanum* was detected. This species' occurrence was probably due to the proximity of the mouth of the river.

This subgroup was represented primarily by *Hydrobia ulvae* (accessory constant; see classification in

Table 2), Scrobicularia plana (exclusive common), Cerastoderma edule (common occasional), and Rissoa parva (very common occasional). The FxD value and the dominance indices indicated that *H. ulvae* is most characteristic of this subgroup (Table 7).

Subgroup A2 was located in the intertidal zone on the border of the inlet. It comprised 18 stations in which a total of 29 species were found (Table 7). It had higher mean percentages of gravel and coarse sand than of medium and fine sands. The mean percentage of carbonates $(7.22\% \pm 0.86\%)$ and the mean diversity value (2.77 ± 0.86) were the highest in the area. The evenness values fluctuated from 0.09 (station I139) to 0.43 (station I131) and the number of

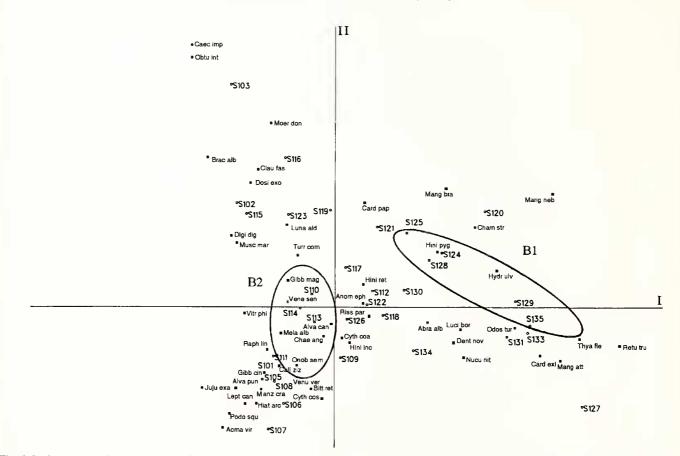


Fig. 6. Stations and species arranged according to axes I and II of the correspondence analysis (DCA) for the subtidal stations, showing the division into two main groups, confirmed by the confidence ellipsis method. Species codes as in Table 8.

species varied from 29 (station I103) to six (station I140).

The characteristic species of this subgroup were Gibbula umbilicalis, Littorina obtusata (exclusive constants), L. littorea (elective constant), L. mariae (very common exclusive), Lepidochitona cinera (very common elective), Mytilus edulis (very common occasional), Monodonta lineata, and Patella vulgata (exclusive common). According to the values of FxD and the dominance indices, the most characteristic species of this subgroup were G. umbilicalis, L. littorea, L. obtusata, L. mariae, and L. cinerea (Table 7).

Subgroup A3 was established in the mid-inner area of the inlet, along with two subtidal stations (S132, S104). It encompassed a total of 17 stations which account for 24 species. This group had high mean percentages of fine sand ($45.92\% \pm 25.60\%$) and medium sand ($21.89\% \pm 14.63\%$). The diversity had a lower mean value than in the A2 subgroup (2.35 ± 0.82), evenness varied from 0.09 (station 1133) to 0.92 (station 1119), and species richness varied from 24 (station 1102) to 4 (station 1119).

The most noteworthy species were Parvicardium exiguum (preferential constant), Turbonilla acuta, Chrysallida obtusa (preferential common), Rissostomia *membranacea* (elective common), and *Retusa truncatula* (very common accessory). The FxD index indicated that the most characteristic species of this assemblage were *P. exiguum, T. acuta, C. terebellum*, and *R. membranacea* (Table 7). *Bittium reticulatum* was also present and showed a high dominance and FxD index, making it an important species in the characterization of these bottoms, although it also had a high dominance in subgroups A2 and B2.

Cerastoderma edule, Venerupis senegalensis, and Hydrobia ulvae also had high FxD index values in subgroup A2. This shows that there were three important species in the characterization of these intertidal bottoms.

Subgroup B1 was located in the mid-outer subtidal zone of the inlet. It was comprised of ten stations with a total of 31 species. It had relatively high mean percentages of gravel (22.47% \pm 1.99%) and fine sand (21.29% \pm 20.01%). The percentage of carbonates was lower than in subgroup B2. The mean diversity value was high (3.07 \pm 0.62) and evenness fluctuated from 0.94 (station S124) to 0.56 (station S125). The number of species varied from 26 (station S133) to 8 (station S135).

This subgroup was primarily composed of *Thyasira flexuosa* (preferential constant), *Hinia reticulata* (occasion-

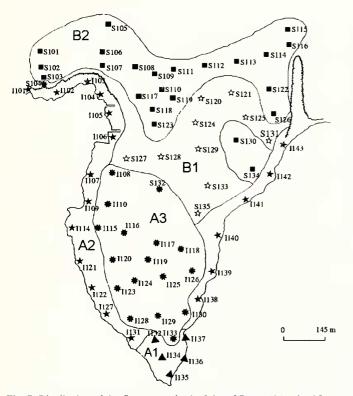


Fig. 7. Distribution of the five groups in the Inlet of Baño. (A1, \blacktriangle ; A2, \bigstar ; A3, \circledast ; B1, \diamondsuit ; B2, \blacksquare)

al constant), *H. incrassata* (very common accessory), *H. pygmaea* (very common preferential), *Abra alba* (very common accessory), *A. nitida* (exclusive common), *Nucula nitida, Mangelia brachystoma*, and *Odostomia turrita* (preferential common). The highest dominance and FxD values were found for *T. flexuosa*, *A. nitida*, and *N. nitida* (Table 8).

Subgroup B2 was located in the outer area of the subtidal zone, excluding stations S134 and S130, which were located in the central area. It was comprised of 23 stations encompassing a total of 70 species. It had a heterogeneous granulometric composition, with the lowest mean percentage of fine sand of all the subgroups ($7.56\% \pm 5.01\%$) and a mean silt-clay value similar to that of subgroup B1 ($21.57\% \pm 12.54\%$). The mean diversity value (3.44 ± 0.61) was slightly higher than in subgroup B1. Evenness values ranged from 0.37 (station S126) to 0.85 (station S101); species richness values ranged from 45 (station S111) to 18 (station S134).

This subgroup was represented by a great number of constant species which were very common, common, preferential, or elective. According to the values of the dominance and FxD indices, the most characteristic species were: Lunatia alderi, Manzonia crassa, Gibbula magus, Leptochiton cancellatus, Calyptraea chinensis, Cytharella coarctaca, Raphitoma linearis, Onoba semicostata, and Venerupis rhomboides (Table 8).

In both subgroups B1 and B2, *Hinia reticulata, H. incrassata, Mysella bidentata*, and *Papillicardium papillosum* had high dominance values as well as high FxD indices. It is also important to note the presence of *Rissoa parva*, which appeared as an occasional constant species in subgroups B1 and B2 and attained high values of dominance and FxD. This latter species also appeared as a very common occasional species in three subgroups of intertidal stations (A1, A2, A3). *Venerupis senegalensis* was also widely distributed. This species had a high FxD index, although it was poorly represented in subgroup B1 (occasional not very common), in B2 (occasional constant), and A3 (accessory constant).

DISCUSSION

Species richness and diversity showed a distinct positive correlation with the sort coefficient and a negative correlation with fine sand content. This is logical because the increase in the sort coefficient implies that there is an increase in the diversity of the particles and an increase in heterogeneity, in agreement with Rhoads and Young (1970), Webb (1976), and Lewis (1982), to name but a few, who stated that spatial heterogeneity is conducive to higher diversity. Cornet (1985), however, reported that the nature of the bottom controls community structure, but that the different sediment parameters do not share equal importance. Rather than the dimensions of the sediment particles, it is the variety of the particles that plays the key role. This reflects the microstructural complexity of the habitat in which an increase in sediment variability allows species diversity to rise (Gray, 1974). Moreover, as the grain size decreases, there are restrictions related to the poor microdiversity of the sediment environment, the limited interstitial space, and oxygen diffusion, which justify the negative correlation between diversity and percentage of fine sand.

A negative correlation was found between diversity and the depth parameter, the former diminishing as depth decreased. This can be attributed to the fact that the fauna inhabiting the intertidal zone must tolerate abrupt environmental changes, being faced with problems resulting from changes in salinity, rough conditions on the intertidal floor, danger of desiccation, and extreme temperatures (Kikuchi, 1987).

In the subtidal zone, the highest values for diversity and species richness were found in the stations where the maërl bed was located (*Lithothamnion* and *Phymatolithon*), a bottom composed of shells with a small amount of mud. According to Urgorri *et al.* (1992), these maërl bottoms are

Species Code Cons Fid Dom Fi0 Cons Fid Dom Fid Cons Fid Dom Fid Did Dom Fid Did Did Did Did Did Did				A1			A2				1	A3	
	becies/ Code	Cons	Fid	Дот		Cons	Fid	Dom	FxD	Cons	Fid	Dom	FxD
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	ttorina littorea (Linné, 1758) [Litt lit*]	14	12.38	0.78	173.30	88	77.87	4.51	6,852.56				
	ibbula umbilicalis (da Costa, 1778) [Gibb umb*]					83	94.31	7.42	7,827.73				
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ttorina obtusata (Linné, 1758) [Litt obt*]					77	100.00	13.37	7,700.00				
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	erastoderma edule (Linné, 1758) [Card edu*]	42	23.72	0.55	996.20	83	46.89	1.75	3,891.87	52	29.37	2.34	1,527.24
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	ydrobia ulvae (Pennant, 1777) [Hydr ulv*]	100	39.37	97.40	3,937.00	88	34.64	19.54	3,048.32	52	20.47	25.27	1,064.44
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	enerupis senegalensis (Gmelin, 1791) [Vene sen]					77	29.27	3.60	2,253.79	88	33.46	3.15	2,944.48
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	ttorina mariae Sacchi & Rastelli, 1966 [Litt mar*]					55	100.00	15.20	5,500.00				
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	pidochitona cinerea (Linné, 1767) [Lepi cin*]					72	72.00	1.36	5,184.00				
	ytilus edulis Linné, 1758 [Myti edu*]	14	8.80	0.27	123.20	72	42.58	7.45	3,260.16	23	14.46	1.08	332.58
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ssoa parva (da Costa, 1778) [Riss par]	57	14.21	0.32	809.90	72	17.95	12.32	1,292.40	94	23.44	28.45	2,203.36
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	ttium reticulatum (da Costa, 1778) [Bitt ret]					99	27.04	2.55	1,784.64	70	28.68	5.38	2,007.60
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	robicularia plana (da Costa, 1778) [Scro pla]	28	100.00	0.18	2,800.00								
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	atella vulgata Linné, 1758 [Pate vul*]					50	100.00	0.61	5,000.00				
$ \left[\begin{array}{cccccccccccccccccccccccccccccccccccc$	onodonta lineata (da Costa, 1778) [Mono lin*]					38	100.00	0.48	3,800.00				
	canthochitona crinita (Pennant, 1777) [Acan cri*]					33	66.00	0.25	2,178.00				
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ysia viridis (Montagu, 1804) [Elys vir*]	14	14.89	0.09	208.40	33	35.10	0.23	1,155.00	47	50.00	1.11	2,350.00
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	hrysallida obtusa (Brown, 1827) [Chry obt]									41	65.07	0.02	2,667.87
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ibbula cineraria (Linné, 1758) [Gibb cin*]					44	28.02	1.03	1,232.88	35	22.29	0.51	780.1
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	urbonilla acuta (Donovan, 1804) [Turb acu*]					27	32.92	0.48	888.84	47	63.51	1.20	2,984.97
	vsella bidentata (Montagu, 1803) [Mvse bid]	14	4.44	0.13	62.16	50	15.87	2.57	793.51	70	22.22	7.39	1,555.4(
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	inia reticulata (Linné, 1758) [Hini ret]	14	4.00	0.04	56.00	50	14.45	3.89	722.50	82	23.69	2.40	1,942.58
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	etusa truncatula (Brugière, 1792) [Retu tru*]					27	19.00	1.72	513.00	52	36.61	2.06	1,903.72
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	bra alba (Wood, 1802) [Abra alb*]									52	29.71	1.11	1,544.92
$\begin{tabular}{ c c c c c c c c c c c c c c c c c c c$	arvicardium exiguum (Gmelin, 1791) [Card exi*]					27	17.53	1.83	468.45	94	61.03	2.46	5,736.82
$ [14 \ 100.00 \ 0.04 \ 1,400.00 \ 16 \ 52.40 \ 16 \ 562.40 \ 16 \ 562.40 \ 16 \ 52.40 \ 16 \ 52.40 \ 16 \ 52.85 \ 1.57 \ 1,382.70 \ 22 \ 6.38.4 \ 17 \ 22 \ 6.38.4 \ 17 \ 22 \ 6.38.4 \ 16 \ 22 \ 31.37 \ 0.10 \ 501.92 \ 35 \ 6.8.6 \ 8.6 \ 28 \ 22 \ 23 \ 17 \ 23.94 \ 0.40 \ 17 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 11 \ 11 \ 11 \ 11 \ 11 \ 11 \$	enus verrucosa Linné, 1758 [Venu ver*]									29	15.42	0.17	447.18
$ [14 \ 25.45 \ 0.04 \ 652.40 \ 160.00 \ 16 \ 1.57 \ 1.382.70 \ 22 \ 62.85 \ 1.57 \ 1.382.70 \ 22 \ 62.85 \ 1.57 \ 1.382.70 \ 22 \ 673.60 \ 16 \ 21.3 \ 22 \ 673.60 \ 17 \ 23.94 \ 0.40 \ 17 \ 23.94 \ 0.40 \ 17 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 13.07 \ 0.14 \ 11 \ 11 \ 13.07 \ 0.14 \ 11 \ 11 \ 13.07 \ 0.14 \ 11 \ 11 \ 11 \ 11 \ 11 \ 11 \ 11 \$	isidium casertanum (Poli, 1791) [Pisi cas]	14	100.00	0.04	1,400.00								
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	hrysallida terebellum (Philippi, 1844) [Chry ter]	14	46.60	0.04	652.40								
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	erithiopsis tubercularis (Montagu, 1803) [Ceri tub]					16	100.00	0.69	1,600.00				
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ellia suborbicularis (Montagu, 1803) [Kell tub]					22	62.85	1.57	1,382.70				
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	osinia exoleta (Linné, 1758) [Dosi exo]	14	12.28	0.04	171.90								
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	rachystomia albella (Lovén, 1843) [Brac alb]					22	33.84	0.23	854.48				
nem] 16 31.37 0.10 501.92 35 68.62 8.62 2 17 23.94 0.40 17 23.94 0.40 17 13.07 0.14 17 13.07 0.14 17 13.07 0.14 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 17 22.07 0.08 18 18 18 18 18 18 18 18 18 18 18 18 18	(vania semistriata/ (Montagu, 1808) [Alva sem]					16	42.10	0.72	673.60				
$\begin{bmatrix} 17 & 23.94 & 0.40 \\ 17 & 13.07 & 0.14 \\ 17 & 13.07 & 0.14 \\ 17 & 22.07 & 0.08 \\ 23 & 12.50 & 0.31 \\ 23 & 12.50 & 0.31 \\ 23 & 24.73 & 0.94 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 16 & 21.91 & 0.54 & 350.56 & 23 & 31.50 \\ 17 & 10 & 0.54 & 350.56 & 23 & 31.50 \\ 18 & 10 & 10 & 10 & 10 \\ 18 & 10 & 10 & $	issostomia membranacea (Adams, 1800) [Riss mem]					16	31.37	0.10	501.92	35	68.62	8.62	2,401.70
17 13.07 0.14 17 23.07 0.08 17 22.07 0.08 17 22.07 0.08 17 22.07 0.08 17 22.07 0.08 18 23 12.50 0.31 23 24.73 0.94 23 356.30 16 29.09 0.07 465.44 16 21.91 0.54 350.56 23 31.50 0.28 16 21.91 0.54 350.56 23 31.50 0.28	oerella donacina (Linné, 1758) [Moer don]									17	23.94	0.40	406.98
tr] 17 22.07 0.08 23 12.50 0.31 14 25.45 0.13 356.30 16 29.09 0.07 465.44 52 31.50 0.31 23 24.73 0.94 16 21.91 0.54 350.56 23 31.50 0.28 16 21.91 0.54 350.56 23 31.50 0.28	noba semicostata (Montagu, 1803) [Onob sem]									17	13.07	0.14	222.19
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	hamelea striatula (da Costa, 1778) [Cham str]									17	22.07	0.08	375.19
14 25.45 0.13 356.30 16 29.09 0.07 465.44 sc mar*] 16 21.91 0.54 350.56 23 31.50 0.28 16 21.91 0.54 350.56 23 31.50 0.28	inia incrassata (Ström, 1768) [Hini inc*]									23	12.50	0.31	287.50
14 25.45 0.13 356.30 16 29.09 0.07 465.44 [Musc mar*] 16 21.91 0.54 350.56 23 31.50 0.28 [16 11.91 0.54 350.56 23 31.50 0.28	nomia ephippium Linné, 1758 [Anom eph*]									23	24.73	0.94	569.25
	oripes lacteus (Linné, 1/58) [Lori lac*]	14	25.45	0.13	356.30	16	29.09	0.07	465.44 250.57	ę	01 50	00.0	
	uscuus marmoratus (Cantraine, 1833) [Musc mar [*]]					10	16.12	0.54	00.000	5	00.15	0.28	124.50

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stable substrata that provide a good shelter for small mollusks, because they have small spaces which favor the settlement of species typical of hard substrata. A large number of these individuals inhabit these bottoms, settling on branches of seaweed. There are also species typical of muddy bottoms which are found in the lower area or in contact with the sandy substratum.

Relatively high values of diversity and species richness were found in the intertidal zone in stations with *Zostera noltii*. The seagrass gives rise to a complex habitat with richer fauna (Peterson *et al.*, 1984), either because it stabilizes the sediment or because it shelters certain species, creating more complex microhabitats which are non-existent in unprotected zones.

The minimum values of species richness and diversity were found in the intertidal stations in proximity to the mouth of the river, owing to the almost exclusive dominance of *Hydrobia ulvae*, which reached high densities. This gastropod enjoys a broad range of food sources, which enables it to thrive in highly varied environments, feeding on organic remains, fecal pellets, or sediment particles, behaving as a detritivore (Jacobs *et al.*, 1983) or an herbivore consuming microalgae obtained by grazing (Muus, 1967). According to Wolff (1973), the high densities of this gastropod are linked to intertidal areas having little water movement and high sediment stability.

Generally speaking, the diversity values observed in the inlet were high. When compared with the results of other benthic studies on mollusks, our values were higher than those found in the Ría de Ares-Betanzos (Troncoso *et al.*, 1993), the Gulf of Gascogne (Cornet, 1985, 1986), and in Raunfjorden (Tunberg, 1981), and were similar to those reported on the southern banks of the Lake of Tunis (Zaouali, 1974, 1981).

Two communities were described in the area under study. However, the sediment heterogeneity in this zone causes the occurrence of phenomena such as facies and transitions. In the subtidal zone (group B), the community of "Syndosmia" (Thorson, 1957) was encountered, structured in facies (B1, B2). This community, settled in the subtidal zone, has been found in several areas: in the Ría de Arousa (Cadée, 1968; Mora, 1980), in the Bay of Santander (Lastra *et al.*, 1990), in populations of the western English Channel (Cabioch, 1968), off the coast of Scotland (Pearson, 1970), in the Rade de Brest (Hily, 1976), and in the Gulf of Normandy-Brittany (Retier, 1979; Gentil, 1982).

The subgroup B1 represents the facies of *Thyasira flexuosa-Nucula nitida*, which is typical of bottoms having fine sediment particles and a high silt-clay ratio. Glémarec (1964) described this facies in the Gulf of Morbihan as the "Nucula turgida type C" facies with N. turgida, Abra nitida, and other species such as T. flexuosa. Subgroup B2

represents a facies in transition toward the community of Clausinella fasciata, having bottoms with larger-sized particles than in B1, but with a relatively high silt-clay ratio, which causes it to be characterized by species both typical of the community of "Abra alba" as well as by species typical of the community of "C. fasciata" (Dosinia exoleta, Pododesmus squamula, Gouldia minima, C. fasciata, Venerupis rhomboides, and Moerella donacina). Also found within this facies (S101, S102, S107, S108) is a maërl bottom, with the above-mentioned typical species present. The accumulation of Lithothamnion and Pymatholiton on the sediment creates a particular algal epifauna and endofauna, which is why many authors have described the facies as belonging to the community of Clausinella fasciata (e. g., Glémarec, 1965; Cabioch, 1968; Keegan, 1974; Mora, 1980).

On the intertidal bottoms (group A) a small community of "Macoma" (Thorson, 1957) was encountered structured in facies (A1, A2, A3). According to Thorson (1957) the small community of "Macoma" (community of *Cerastoderma edule-Scrobicularia plana*) is a variety of the community of *M. balthica*. Although this community has been cited from higher latitudes, in its purest sense, it does not extend beyond the English Channel, where species giving rise to the variety *C. edule-S. plana* become more frequent. In the zone under study, this community was found on bottoms of fine sand. A clear dominance of *Hydrobia ulvae* was seen and high dominance values were also cited in other areas of the European coast (Denis, 1983).

Cadée (1968) and Mora (1980) found similar communities on Galician coasts. In the Ría de Arousa they described a community of "Cerastoderma edule-Scrobicularia plana" in the polyhaline zone. Viéitez (1976) described the same community on the beach of Meira (Ría de Vigo), which is known to settle on bottoms of fine sand with mean values of organic matter of 0.85%. Penas and González (1983) reported the presence of this community in the Ría de Arousa; Planas (1986) studied this community in the Inlet of Lourizán (Ría de Pontevedra) on bottoms primarily composed of a coarse fraction. Junoy and Viéitez (1990) found this community in the Ría de Foz and it was distinguished by favoring bottoms having silt-clay percentages of over 5% and relatively high organic matter content, where some species which were highly abundant, such as Hydrobia ulvae, are typical of estuaries having organic pollution (Viéitez, 1981; Penas and González, 1983; Planas and Mora, 1984b; Planas et al., 1984).

Within this community, subgroup A1 comprises a facies dominated almost exclusively by *Hydrobia ulvae*, and to a lesser extent by *Scrobicularia plana*. *H. ulvae*, which reached the highest macrofaunal abundances in the study area, forms a typical estuarine population that tolerates eurythermal and euryhaline conditions. Subgroup A2

Table 8. Constancy index (%, Cons), fidelity index (%, Fid), dominance (Dom), and fidelity-dominance product (FxD) in subgroups B1 and B2. (*, species present in at least 10% of the stations).

]	B1				B2	
Species/ Code	Cons	Fid	Dom	FxD	Cons	Fid	Dom	FxD
Lunatia alderi (Forbes, 1838) [Luna ald*]					78	88.63	0.39	6,913.14
Cytharella coarctata (Forbes, 1840) [Cyth coa*]	40	31.74	1.50	1,269.60	86	65.66	1.80	5,646.76
Turritella communis Risso, 1826 [Turr com]	50	36.76	0.46	1,838.00	86	63.00	2.36	5,418.00
Calyptraea chinensis (Linné, 1758) [Caly chi*]	60	41.00	1.04	2,460.00	86	58.90	2.84	5,065.40
Onoba semicostata (Montagu, 1803) [Onob sem*]	30	23.00	0.46	690.00	78	60.00	10.04	4,680.00
Papillicardium papillosum (Poli, 1795) [Card pap*]	80	47.90	6.82	3,832.00	82	49.10	3.55	4,075.40
Hinia incrassata (Ström, 1768) [Hini inc*]	70	38.00	6.01	2,660.00	86	46.70	5.35	4,016.50
Cerastoderma edule (Linné, 1758) [Card edu]					80	49.77	1.67	3,981.87
Gibbula cineraria (Linné, 1758) [Gibb cin*]					78	49.68	2.87	3,875.00
Venus verrucosa Linné, 1758 [Venu ver*]					78	45.34	1.23	3,536.52
Hinia reticulata (Linné, 1758) [Hini ret]	100	28.90	10.98	2,890.00	100	28.90	4.66	2,890.00
Mysella bidentata (Montagu, 1803) [Myse bid]	90	28.57	23.93	2,571.30	91	28.80	24.69	2,628.08
Bittium reticulatum (da Costa, 1778) [Bitt ret]	30	12.29	0.46	368.70	78	32.00	3.00	2,496.00
Venerupis senegalensis (Gmelin, 1791) [Vene sen]	20	7.60	0.23	152.00	78	29.65	5.41	2,312.70
Rissoa parva (da Costa, 1778) [Riss par]	100	24.93	4.39	2,493.00	78	19.45	3.47	1,517.10
Manzonia crassa (Kanmacher, 1798) [Manz cra*]					69	93.24	2.06	6,433.56
Gibbula magus (Linné, 1758) [Gibb mag*]					60	100.00	0.43	6,000.00
Leptochiton cancellatus (Sowerby, 1840) [Lept can*]					60	92.30	0.75	5,538.00
Venerupis rhomboides (Pennant, 1777) [Vene rho*]	20	20.83	0.57	416.60	65	67.70	0.84	4,400.50
Alvania punctura (Montagu, 1803) [Alva pun*]					52	83.87	1.56	4,361.24
Clausinella fasciata (da Costa, 1778) [Clau fas*]					52	82.53	0.61	4,291.56
Raphitoma lineraris (Montagu, 1803) [Raph lin*]					52	100.00	0.26	5,200.00
Dosinia exoleta (Linné, 1758) [Dosi exo*]	20	17.54	0.46	350.80	69	60.52	0.90	4,175.80
Hiatella arctica (Linné, 1767) [Hiat arc*]					56	55.40	0.74	3,104.64
Gouldia minima (Montagu, 1803) [Goul min*]	40	43.47	1.15	1,738.80	52	56.52	0.64	2,939.04
Hinia pygmaea (Lamarck, 1822) [Hini pyg*]	70	57.37	1.73	2,660.00	52	42.60	0.54	2,215.20
Abra alba (Wood, 1802) [Abra alb*]	60	34.28	4.50	2,056.80	52	29.71	1.36	1,544.92
Abra nitida (Müller, 1776) [Abra nit]	40	100.00	2.42	4,000.00				
Mangelia nebula (Montagu, 1803) [Mang neb*]	30	78.94	0.46	2,368.20				
Acmaea virginea (Müller, 1776) [Acma vir*]					34	100.00	0.29	3,400.00
Vitreolina philippii (Rayneval & Ponzi, 1854) [Vitr phi*]					26	100.00	0.08	2,600.00
Melanella alba (da Costa, 1778) [Mela alb*]					47	82.45	0.34	3,875.15
Pododesmus squamula (Linné, 1758) [Podo squ*]					39	88.63	5.52	3,456.57
Digitaria digitaria (Linné, 1758) [Digi dig*]					39	79.59	0.19	3,104.01
Brachystomia albella (LovÈn, 1843) [Brac alb*]					43	68.25	0.08	2,600.00
Jujubinus exasperatus (Pennant, 1777) [Juju exa*]					30	75.00	0.44	2,250.00
<i>Caecum imperforatum</i> (Kanmacher, 1798) [Caec imp*]					26	83.80	0.09	2,178.80
Obtusella intersecta (Wood, 1856) [Obtu int*]					26	72.00	0.01	1,760.20
Moerella donacina (Linné, 1758) [Moer don*]					39	54.92	0.19	2,141.88
Myrtea spinifera (Montagu, 1803) [Myrt spi]	20	20.00	0.23	400.00				_, _
Lucinoma borealis (Linné, 1767) [Luci bor*]	20	31.25	0.23	625.00	34	53.12	0.09	1,806.08
Anomia ephippium Linné, 1758 [Anom eph*]	20	21.50	1.61	430.00	39	41.93	3.04	1,635.27
Mangelia brachystoma (Philippi, 1844) [Mang bra*]	40	57.14	0.92	2,285.60	30	42.87	0.11	1,286.10
<i>Chamelea striatula</i> (da Costa, 1778) [Cham str*]	30	38.96	1.15	1,168.80	30	38.96	0.21	1,168.80
Nucula nitida Sowerby, 1833 [Nucu nit*]	50	65.78	1.15	3,289.00	26	34.21	0.08	889.46
Musculus marmoratus (Cantraine, 1835) [Musc mar*]	50	05.70	1.15	5,207.00	34	46.57	0.32	565.80
	100	64.93	15.72	6,493.00	43	27.92	0.40	1,200.99
Thyasira flexuosa (Montagu, 1803) [Thya fle*]	20	12.57	0.23	975.60	30	18.86	0.23	889.46
Mytilus edulis Linné, 1758 [Myti edu*]	20	12.57	0.25	975.00	17	100.00	0.13	1,700.00
Gibbula tumida (Montagu, 1803) [Gibb tum]					17	100.00	0.13	1,700.00
Alvania beani (Thorpe, 1844) [Alva bea]							0.12	1,700.00
Alvania cancellata (da Costa, 1778) [Alva can*]					17	100.00		
Caecum glabrum (Montagu, 1803) [Caec gla]					17	100.00	0.05	1,700.00
Haedropleura septangularis (Montagu, 1803) [Haed sep]					17	100.00	0.03	1,700.00
Odostomia conspicua Alder, 1850 [Odos con]					13	100.00	0.06	1,300.00
Monia patelliformis (Linné, 1767) [Moni pat]					13	100.00	0.04	1,300.00
Brachystomia eulimoides (Hanley, 1844) [Brac eul]					13	100.00	0.03	1,300.00

(continued)

		I	31			I	32	
Species/ Code	Cons	Fid	Dom	FxD	Cons	Fid	Dom	FxD
Callochiton achatinus (Montagu, 1803) [Call ach]					13	100.00	0.02	1,300.00
Calliostoma zizyphinum (Linné, 1758) [Call ziz*]					21	67.00	0.07	1,407.00
Dentalium novencostatum Lamarck, 1838 [Dent nov*]					21	67.00	0.06	1,407.00
Diodora graeca (Linné, 1758) [Diod gra]					13	100.00	0.03	1,300.00
Chrysallida indistincta (Montagu, 1808) [Chry ind]					13	72.20	0.03	938.60
Chaetopleura angulata (Splenger, 1797) [Chae ang*]					21	58.00	0.06	1,218.00
Cytharella costata (Donovan, 1803) [Cyth cos*]	20	48.78	0.23	975.60	21	51.21	0.13	1,075.41
Mangelia attenuata (Montagu, 1803) [Mang att*]	20	60.60	0.46	1,212.00	13	56.52	0.02	734.76
Alvania semistriata (Montagu, 1808) [Alva sem]					17	44.73	0.78	760.41
Acanthochitona crinita (Pennant, 1777) [Acan cri]					17	34.00	0.05	578.00
Kellia suborbicularis (Montagu, 1803) [Kell sub]					13	37.14	0.03	482.82
Odostomia turrita Hanley, 1844 [Odos tur*]	30	57.69	0.92	1,730.70	17	32.69	0.11	555.73
Chrysallida obtusa (Brown, 1827) [Chry obt]					17	29.63	0.05	452.71
Ostrea edulis Linné, 1758 [Ostr edu]					13	28.88	0.02	375.44
Lepidochitona cinerea (Linné, 1767) [Lepi cin]					17	17.00	0.12	289.00
Retusa truncatula (Bruguière, 1792) [Retu tru*]	50	35.21	1.04	1,760.50	13	9.10	0.03	118.30
Parvicardium exiguum (Gmelin, 1791) [Card exi*]	20	12.98	0.23	152.00	13	8.40	0.08	109.20
Hydrobia ulvae (Pennant, 1777) [Hydr ulv*]	20	7.50	0.21	150.00	13		0.04	63.89

constitutes another facies within the community of "Macoma," settled on bottoms having coarser sediment with a low silt-clay content. Cadée (1968) found a similar fauna in the shallow border area of the Ría de Arousa, but this author integrated it into a community of "Tellina" (Thorson, 1957). However, according to Cadée (1968), the resemblance is not exact, because the genera characteristic of this community are not found very often, but rather the area, in addition to the dominant presence of the typical species of this community, has other species characteristic of fine substrata, where there are stones to which algae become attached thus providing food for Littorina littorea, L. obtusata, Gibbula umbilicalis, etc. The fauna belonging to this facies can be associated with the intertidal zone of Laminaria reported by Jeffreys (1863). Subgroup A3 consists of a facies located in an area with a relatively high siltclay content and where Zostera noltii settles. The biocenotic classification of these bottoms is difficult, because, as explained by Pérès (1958), the community of Zostera is a complex community where three compartments can be distinguished: the sessile or sedentary population of the leaves, the sediment population, and the vagile population living in the shade of the leaves. Currás and Mora (1991) stated that these bottoms should be associated with a particular biocenosis with endofauna typical of nearby populations and lacking a vegetative covering. Petersen (1918) reported that the nature of the epifauna of Zostera is determined by the type of animal community where it settles. Pérès and Picard (1964) included the facies of Z. noltii within the biocenosis of superficial silty sands in the calm zones. Muus (1967) studied the bottoms of Zostera and considered the fauna as an animal community corresponding to the community of "Macoma." The results concur with the opinion of Currás and Mora (1991), because upon analyzing the most significant species in this subgroup, it can be seen that it is a facies of the small community of Macoma, with an endofauna characteristic of this community (Loripes lacteus, Cerastoderma edule, and Venerupis senegalensis) and an epifauna of euryhaline species such as Hydrobia ulvae, Bittium reticulatum, and Rissostomia membranacea.

Another important aspect is the determination of the environmental factors that affect the settlement of the communities. Penas and González (1983), Currás and Mora (1991), and Bachelet and Dauvin (1993), to name but a few, considered that the proportion of the different granulometric classes, silt-clay content, organic matter, and the presence or absence of vegetative cover are the determining factors in the structuring of benthic communities. Our data coincide with the results of the above-mentioned authors, because in the subtidal zone the physico-chemical factors that will be more important in faunal distribution are the sediment gradient and the organic matter content. This is to be expected because this is a narrow bathymetric range, the variation of other physical parameters (temperature, salinity), as pointed out earlier by Jones (1950: 293), will be small, and the decisive factor will be the granulometry of the bottom which is a consequence of the peculiar hydrodynamic regime in the area.

In addition to the granulometric nature of the substratum in the intertidal zone, which is one of the most important factors in the distribution of the species, depth plays an important role in the distribution of the species because the higher intertidal levels present rougher conditions for aquatic organisms. The almost total absence of water during the emersion period prevents them from using this environment to be active and to feed during this period, during which time there is an increased danger of desiccation and freezing. This is why the species on the higher levels have morphological, physiological, ecological, or ethological adaptations that are different from species living at lower levels. The importance of tidal level and zoning, because this implies different types of adaptations, has also been discussed by several authors (Wolff, 1973; Raffaelli and Boyle, 1986; Viéitez and Baz, 1988; Penas and González, 1983; Eleftheriou and Robertson, 1988; Junoy and Viéitez, 1990).

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